ENVIRONMENTAL DETERMINANTS OF EARTHWORM ABUNDANCE IN A TROPICAL CLOUD FOREST

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Abstract: Earthworms are of major importance to soil fertility and ecosystem productivity. Temperature, moisture, and organic litter are all potentially important to earthworm populations. I hypothesized that soil temperature and moisture would be particularly important for earthworm abundance in the Monteverde cloud forest in Costa Rica. I predicted that relatively warm temperatures would tend to increase earthworm abundance and that soil moisture would commonly be so high that it limits earthworm populations (by interfering with aerobic respiration). As predicted, more earthworms were found at lower elevations (higher soil temperature) and on the downhill side of trees (lower soil moisture). Current trends of climate change seem likely to increase earthworm abundance in upper elevations of the Monteverde cloud forest, which may have broad consequences for the detritus-based ecosystem.

Key Words: litter-trap theory, Lumbricidae, Oligochaeta, *soil moisture*

INTRODUCTION

The earthworm (Oligochaeta: Lumbricidae) has earned the title of "nature's tiller" thanks to its contributions towards aeration and mineralization in soil systems. In the upper 15 - 35 cm of soil, earthworms alter both physical and chemical conditions to enhance soil fertility and ecosystem productivity (Brady and Weil 1996). This ecosystem function could be especially important in tropical regions where soil quality is generally low (Forsyth and Miyata 1984).

Soil temperature, moisture, and availability of organic material are three important factors for earthworm distribution. Earthworms are generally thought to grow best in moist, fresh organic matter at warm temperatures. In temperate zones, maximum earthworm activity occurs during the spring and autumn due to the combination of relatively warm temperatures, high soil moisture, and high organic content from autumnal litter input. Brady and Weil (1996) suggest that earthworms tend to dominate the soil fauna in tropical regions with ≥ 800 mm of annual rainfall, such as the Monteverde cloud forest in Costa Rica (precipitation at Monteverde = 2000 – 3000 mm per year, Janzen 1983). In cloud forests, moisture may not be a limiting factor for earthworms; in fact, excessive moisture could even be detrimental to the worms when water saturation constrains aerobic metabolism.

Deem et al. (1998) found that soil temperature was lower, litter depth was higher, and total soil organic matter was higher at high elevations compared to low elevations at Monteverde. I hypothesized that temperature and moisture should be more important for earthworms in a tropical cloud forest than organic matter (which is very high throughout the cloud forest). I predicted that earthworm abundance would be lower at high elevations than at mid elevations because of excessive soil moisture and lower soil temperatures at higher altitudes. The altitudinal comparison by itself, however, cannot separate the effects of soil temperature, soil moisture, and litter quality because these factors co-vary across elevation. Because tree trunks trap litter and constrain drainage, soil on the uphill side of trees is higher in nutrients and more saturated with moisture than soil on the downhill side (Janzen 1983, Carson et al. 1995). Considering these fine scale differences between soil habitats, I included comparisons of worm abundance on the uphill and downhill sides of trees within each altitude. If soil moisture becomes excessive for earthworms, there should be a lower abundance of worms on the wetter uphill side of trees despite higher organic matter and similar temperatures compared to the downhill side.

METHODS

From 21 – 23 January 2000, I sampled earthworm abundance and soil characteristics on the uphill side and downhill side of 10 trees at each of two different elevations in the cloud forest of the Estación Biológica Monteverde, Monteverde, Costa Rica. Study trees of ≈ 30 cm dbh with low to moderate buttressing were haphazardly selected at each of two elevations: 1530 to 1580 m asl (mid elevation), and 1730 to 1780 m asl (high elevation).

On the uphill side and downhill side of each tree, I designated a 28 x 28 cm plot 5 cm from the point of soil-bark contact. Soil temperature was measured at 8 cm depth in the center of each plot prior to soil disturbance. I then searched the soil to a depth of 15 cm with a trowel and bare hands for 3 min, and recorded the number of lumbricid worms within each plot. Soil moisture measurements collected with a hygrometer (Demetra System Soil Tester) were discarded because replicate measurements of the same soil were as variable as plots and sites (apparently due to the unusually high soil moisture and/or defects of the hygrometer).

Worm abundance and soil temperature were analyzed with an ANOVA model that included tree side (uphill vs. downhill), elevation, tree side x elevation, and tree nested within elevation (mid vs. high). Worm abundance data were normalized with a common log transformation.

RESULTS

Earthworm abundance was higher in the mid-elevation sites compared to the high-elevation sites, and also on the downhill side of trees compared to the uphill side (Fig. 1; $F_{1,18} = 51.75$, $p < 0.001$; $F_{1,18} = 4.80$, $p = 0.042$; main effects of elevation and tree side, respectively). There was no interaction between tree side and elevation ($F_{1,18} = 0.68$, $p = 0.42$), and individual trees within an elevation did not differ in worm abundance ($F_{1,18} = 1.54$, $p = 0.18$). As expected, temperature was also

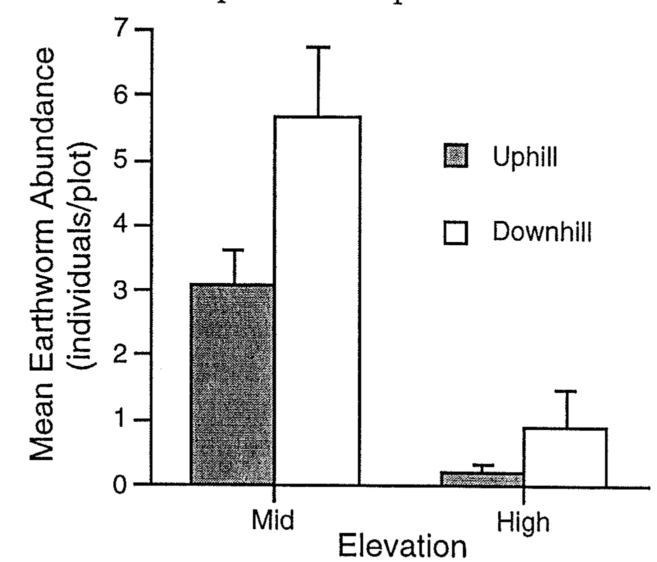

Figure 1. Mean earthworm abundance (± SE) in 28 x 28 cm plots uphill and downhill of tree boles at mid and high elevations in Monteverde cloud forest, Costa Rica (n = 10 trees per elevation).

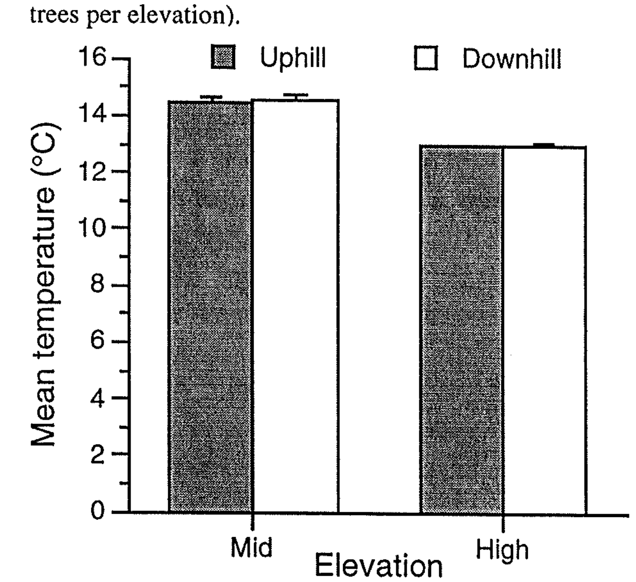

Figure 2. Mean soil temperature (± SE) uphill and downhill of tree boles at mid and high elevations in Monteverde cloud forest, Costa Rica (n = 10 trees per elevation).

higher in mid-elevation compared to high-elevation sites (Fig. 2; $F_{1,18} = 86.66$, $p < 0.001$). Within an elevation, temperatures tended to be slightly warmer below trees than above trees ($F_{1,18} = 3.27$, $p = 0.087$), but the magnitude of the effect was so small as to be biologically inconsequential (least square means differed by 0.11° C at mid elevation and 0.02° C at high elevation; Fig. 2). Soil temperatures differed significantly among trees within a site ($F_{1,18} = 22.16$, $p < 0.001$), but again the effect was relatively small (range of ≈ 1.5° C between warmest and coolest trees within each elevation).

Discussion

Results supported the hypothesis that earthworm abundance in a montane tropical forest is influenced by temperature and moisture. Significantly fewer worms were found at higher elevations than at lower elevations, which is correlated with the decrease in soil temperature and increase in moisture at higher elevations. Of course, these correlative data do not demonstrate causation, and there is a plethora of plausible possible causes for elevational patterns in earthworm abundance because many factors vary within elevation. Significant differences in earthworm abundance between the uphill and downhill sides of individual trees were more surprising and informative. It seems likely that lower earthworm abundance on the uphill side is caused by an excess of soil moisture. If earthworms were moisture limited or were responding to litter input, there should have been higher abundance in the moist, litter-rich environment of the uphill side. Furthermore, if soil temperature is the main determinant of local worm abundance, we would not have expected any difference between uphill and downhill sides of trees. Excessive soil moisture at Monteverde could exert negative effects on earthworms through either a direct effect on aerobic metabolism or an indirect effect on food quality (dissolved organic matter). Accurate soil moisture measurements would be useful in directly testing the effect of excessive soil moisture on earthworm abundance.

These patterns in earthworm abundance contribute to our understanding of the detritus-based ecosystem of the Monteverde cloud forest. For example, Pounds et al. (1999) argued that recent amphibian extinctions at Monteverde are the result of a climatic trend towards increased temperatures and decreased moisture in the cloud forest. My results suggest that such a climatic pattern would tend to increase earthworm abundance at high, and possibly mid, elevations of Monteverde. Any changes in the earthworm population would likely affect soil systems including microbial populations and other detritivores. The impacts of such changes would probably include plant communities and might extend to vertebrate consumers of detritivores such as insectivorous birds, reptiles, and amphibians.

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